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A new species of *Lepidotrigona* (Hymenoptera: Apidae) from Thailand with the description of males of *L. flavibasis* and *L. doipaensis* and comments on asymmetrical genitalia in bees

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Abstract

We describe *Lepidotrigona satun* Attasopa and Bänziger new species from southern Thailand based upon associated males and females (workers). The new species is a member of the *L. ventralis* species group, which is otherwise represented in Thailand only by *L. flavibasis* and *L. doipaensis*. We also describe the males of the latter two species, associated with nests from close to their type localities in northern Thailand. *Lepidotrigona doipaensis* Schwarz and *L. flavibasis* (Cockerell) had previously often been misidentified as *L. ventralis* (Smith), a species confirmed only from Borneo. Based upon differences in male morphology, especially of the metasomal sterna, we conclude that the male described from Vietnam by Sakagami (1975) as belonging to *L. flavibasis* represents an undescribed species. Our findings support previous taxonomic studies that highlight the importance of including males in the differentiation of closely related species of meliponines and their association with workers. The three species whose males we describe have asymmetric penis valves with the asymmetry differentially developed among the three. We compare this genitalic asymmetry with that known from a different apid genus, *Tarsalia*.

Key words: Asymmetry, *L. satun* **n. sp.**, *L. ventralis*, stingless bees, taxonomy, *Trigona*

Introduction

The genus *Lepidotrigona* Schwarz, 1939 is in dire need of revision, with different authors accepting very different species delimitations (compare Rasmussen 2008 who suggests 12 described species with Ascher & Pickering 2017 who recognize only four species). In this paper, we describe a new species from Thailand from the male and the worker. Furthermore, we describe the males of two more species from close to their type localities and contrast our findings with those of Sakagami (1975).

The main references for earlier treatments of these bees are Schwarz (1939), Sakagami (1975) and Rasmussen (2008, 2013). Our new species belongs to the group of smaller species of the genus, called the "*ventralis* species group" by Rasmussen (2008). This species group consists of *Lepidotrigona arcifera* (Cockerell, 1929), *L. doipaensis* Schwarz, 1939, *L. flavibasis* (Cockerell, 1929), *L. hoozana* (Strand, 1913), and *L. ventralis* (Smith, 1857). Various synonymies and status changes in these taxa were briefly discussed by Rasmussen (2013). Unfortunately, the two species currently known from Thailand, *L. doipaensis* and *L. flavibasis*, were traditionally considered as subspecies of *L. ventralis*, so that they were often mentioned simply as *L. ventralis* in studies not concerned with taxonomy. However, despite over 10 years of studying stingless bees in Thailand, one of us (H.B.) has never seen *L. ventralis* s.s. in the country. We doubt that this morphologically distinct species, described based upon material from Borneo (from where some specimens are available to us), occurs in Thailand. True *L. ventralis* workers have pale hairs fringing the dorsal surface of the metatibia (Smith 1857; Schwarz 1939; Rasmussen 2013)

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while these are black in *L. doipaensis* and *L. flavibasis* workers. Moreover, examination of genitalia and sterna of males associated with workers of both these species (see descriptions below) from close to their type localities (see discussion) show that the two are clearly separable as good species without intergradation (Bänziger unpublished data) and they also form clearly distinct clusters based on DNA barcode data (Attasopa, Bänziger, Disayathanoowat & Packer, unpublished data). They are partly sympatric, although somewhat separated by altitude with *L. doipaensis* at about 500–1100 m a.s.l. and *L. flavibasis* at about 925–1700 m a.s.l. In three localities (two on Mount Suthep, the type locality of *L. flavibasis*, and a third in the Sankamphaeng-Doi Saket-Mae On area, approximately 40 km away) their nests were found only a few metres apart, certainly within flight range, but the two species retain the typical morphological differences as described below.

Bänziger *et al.* (2011) discovered a species of *Lepidotrigona* near *L. flavibasis* in southern Thailand. *Lepidotrigona flavibasis* is otherwise unknown from that part of the country. Some of the nests of this species have extremely long, pendulous, 'alpenhorn'-shaped nest entrance tubes of up to 51 cm (Bänziger *et al.* 2011, Fig. 7). These findings prompted H.B. and L.P. to have specimens submitted for DNA barcoding in 2012. Results were unexpected on two counts. First, we found no significant difference in the DNA barcodes between specimens from long and short tubed nests in southern Thailand. Second, there was a sequence divergence of over 10% between these southern samples and *L. flavibasis* from near its type locality in northern Thailand. Morphological analysis of the genitalia and sterna of males caught while leaving the nest of a *Lepidotrigona* near *flavibasis* in southern Thailand provided morphological confirmation of the DNA barcode result suggesting that this is a new, undescribed species different from the other two which, in Thailand, are known only from the north.

Materials and methods

Only wild nests were surveyed as we consider specimens from managed hives unreliable for primary taxonomic research because of uncertainty as to the original location of their provenance. It seems highly unlikely for any of our type or topotype samples to be of feral colonies derived from managed ones because meliponicultures are both geographically distant from our study sites and the practice is a relatively recent one in the country. Elevations were measured with an anaeroid altimeter (5000 m; Thommen, Switzerland), resolution 10 m, calibrated with elevations from maps. *Lepidotrigona* were caught as they flew out of nest entrances undergoing normal activities. Information in material described is transcribed from the original labels in the format, "country, province, location, elevation, collecting date, collector name (nest, number and sex of specimens, comment)". Bees were briefly anaesthetized with ethyl acetate and sexed. The vast majority were workers and so eventually mostly released, although all males were kept. A few specimens of both sexes were immediately pickled in 95% ethyl alcohol for subsequent DNA analysis. The remaining males and workers were retained as pinned specimens. The apical half of the metasoma of some males was dissected for genitalic examination. After clearing in 10% KOH for 1–2 hours at 50° C, the segments were preserved in glycerin in microtubes pinned with the male, or as permanent mounts in euparal. For the latter, plastic chips were placed between microscope slide and cover slip to prevent squeezing and deformation of the genitalia.

Full lists of material studied are provided for each of the species in the descriptions below, though the vast majority of the material discussed below is with H.B. at the address given above. In the lists of material studied, GP refers to genitalia preparation with the associated numerical code for that preparation. Museum acronyms and curators assisting with material that aided in our research or where material will be deposited are as follows:

AMNH	American Museum of Natural History, USA (Jerome G. Rozen, Jr., Corey Shepard Smith & Hadel Go)
BMNH	Natural History Museum, UK (David G. Notton)
NBC	Naturalis Biodiversity Center, NL (Frédérique Bakker & Wendy Van Bohemen)
NMNH	Smithsonian National Museum of Natural History, USA (Patricia Gentili-Poole & Seán G. Brady)
PCYU	Packer Collection at York University, CA (Laurence Packer)
QSBG	Queen Sirikit Botanical Garden, THA (Wichai Srisukha)
ROM	Royal Ontario Museum, CA (Christopher Darling & Antonia Guidotti)
ZHMB	Museum für Naturkunde, GER (Michael Ohl, Stephan Junker & Lukas Kirschey)

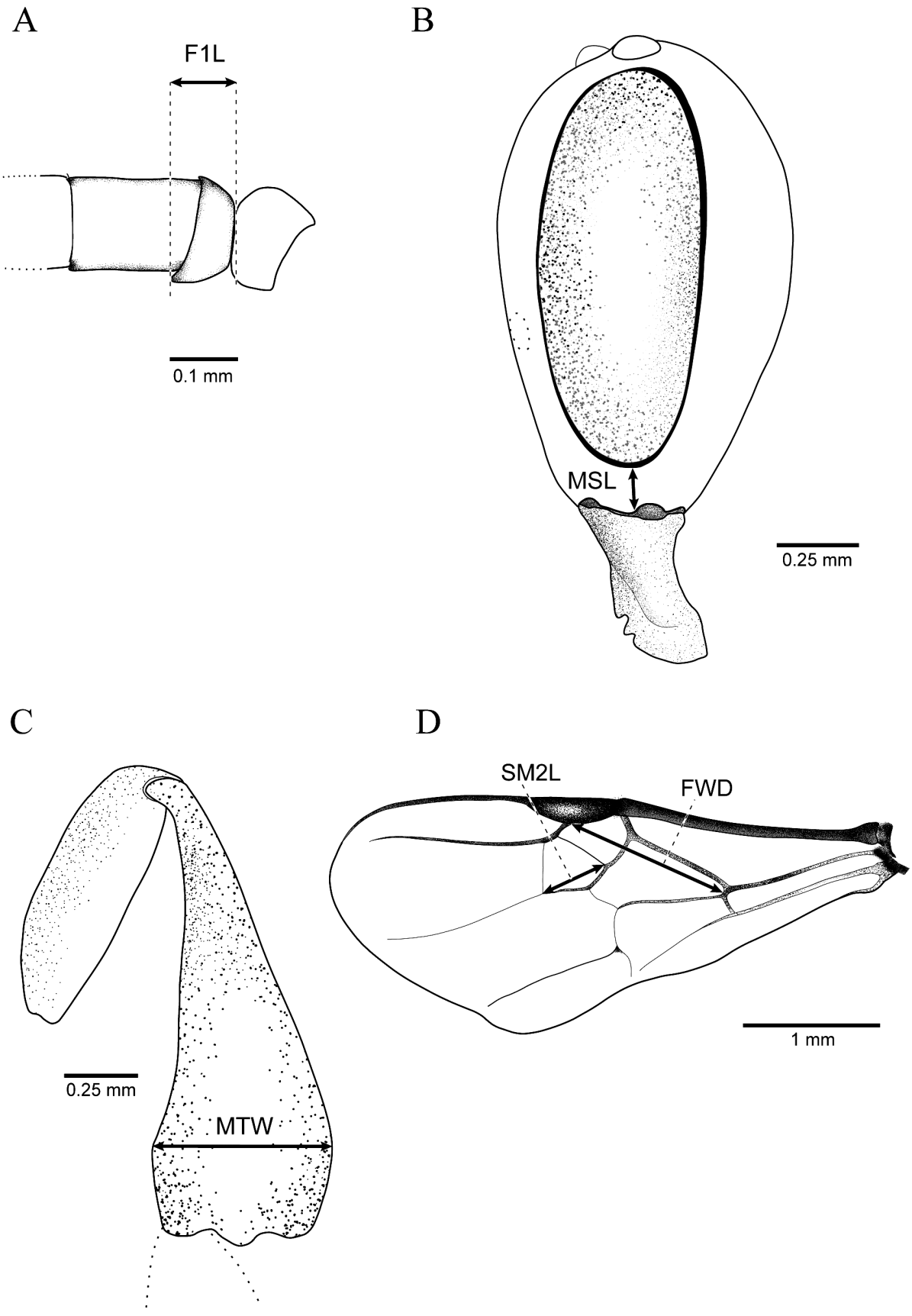

FIGURE 1. Measurements as indicated in the diagnosis and table. (A) pedicel, F1 and F2; (B) head, side view; (C) left metafemur and tibia; (D) left forewing.

Morphology was studied using a Nikon SMZ1500 and images were taken with a Visionary Digital BK plus system with a Canon 40DSLR camera and processed with Photoshop (vers. CS6, Adobe Inc.). Incident light was used for external morphological features, but a combination of incident and transmitted light was used for images of male sterna and genitalia. Figure 1 was drawn by K.A. A range of morphometric variables was assessed, chosen based on earlier studies of stingless bees by Sakagami (1978) and Dollin *et al.* (2015). We present results only for those that were most discriminating among the new and the two other species of the *L. ventralis* species group that we know occur in Thailand. The variables we found to be less discriminating (with extensive or partial overlap either as raw measurements or as ratios) were: body length, head length and width, eye width, gena width, interocellar and ocellocular distance, upper and lower interorbital distance, scape length (with or without the basal bulb), 2nd flagellomere length and width, forewing width, length of 1st submarginal cell, metatibia length, and metabasitarsus length and width. The exact locations of the landmarks used to delimit the retained measurements are shown in Fig. 1. Morphological terminology follows Michener (2007) with the following exceptions: F, S and T refer to flagellomere, and metasomal sternum and tergum respectively, with the number following the letter indicating which one. We use the term metapostnotum instead of propodeal triangle. We refer to surfaces of the legs with the terminology of Aguiar and Gibson (2010). Thus, what Smith (1857) called the upper surface of the hind tibia and Schwarz (1939) and Rasmussen (2013) called the posterior surface, we term the dorsal surface. Similarly, the inner surface of the hind tibia (e.g. Michener 2007) is the posterior surface. Other acronyms used in Fig. 1 and Table 1 are as follows: F1L = F1 length, MSL = malar space length, FWD = forewing diagonal (Sakagami 1978), SM2L = 2nd submarginal cell length, and MTW = metatibia width. The posteromedian emargination of S5 was measured based upon the sclerotized portion only, the apicolateral setae were not included.

Results

Lepidotrigona satun Attasopa and Bänziger n. sp.

Figs. 2: A1–4, 3: A1–A4 & 4–6

Diagnosis. *Lepidotrigona satun* is a member of the "*ventralis*" species group based primarily on size: body and forewing length each less than 5 mm. It is the only species in the group known from the lower peninsula of Thailand. Males can be differentiated from those of the other two species of the "*ventralis*" group confirmed as occurring in Thailand (*L. flavibasis* and *L. doipaensis*) based upon external morphology as follows: margin of mesoscutum of *L. satun* with plumose, scale-like, yellow hairs (Fig. 4: A) (no such hairs in the other two species). S4 of *L. satun* is angularly emarginate apicomedially (Fig. 2: A1) (convex medially and bisinuate laterally in *L. flavibasis*, slightly concave in *L. doipaensis*). The apicosubmedial lobes of S5 in *L. satun* are apically rounded each with 4–7 thick, long setae (Fig. 2: A2) (the lobes are pointed in the other two species and bear only 1–2 setae which are very short in *L. flavibasis* (Fig. 2: B2) or with one very long and, if present, a second much shorter in *L. doipaensis* (Fig. 2: C2)). S5 gradulus does not touch the antecosta in *L. satun* (Fig. 2: A2) whereas it does touch it in the other two species, briefly in *L. flavibasis* (Fig. 2: B2) and extensively in *L. doipaensis* (Fig. 2: C2).

Males can also be differentiated from those of these other two species because of the very short malar space of *L. satun*, at most 0.16 times as long as the length of the first flagellomere whereas in the other two species it is at least 0.27 times as long as the first flagellomere. The ratio of the forewing diagonal to the length of the 2nd submarginal cell also varies among the three: it is largest (≥2.3) in *L. satun*, but at most 2.11 in the other two species (shortest - 1.94 to 2.05 - in *L. doipaensis* and intermediate - 2.05 to 2.11 - in *L. flavibasis*) (see Table 1). The genitalia are also very different in the three species (see below and Fig. 3).

Workers of *L. satun* can be differentiated from all others in the *L. ventralis* species group, except *L. flavibasis*, due to the coloration of the pubescence. *Lepidotrigona satun* has dark hairs on the tibiae and pale yellowish brown to pale brown hairs on the vertex and mostly pale hairs (except posteriorly) on the mesoscutellum; no other member of the *ventralis* species group (except *L. flavibasis*) has this combination: *L. hoozana* and *L. ventralis* have some or entirely (respectively) whitish hairs on the metatibia, whereas the other four species have brown to black hairs; *L. arcifera* has pale hairs on the pro- and mesotibiae whereas *L. satun*, *L. flavibasis* and *L. doipaensis* have dark hairs; *L. doipaensis* has black hairs on the vertex and mesoscutellum, whereas *L. flavibasis* and *L. satun* do not have these hairs black but yellowish grey or variously pale to dark brown, respectively; the thickest of these hairs

are about 0.007 mm, 0.003 mm and 0.005 mm wide, respectively. Workers of *L. satun* and *L. flavibasis* can be readily differentiated by the ratio of lengths of the metatibia and 2nd submarginal cell, at least 1.21 in *L. satun*, at most 0.98 in *L. flavibasis* and intermediate 1.05–1.09 in *L. doipaensis*. There are additional morphometric differences among the three species (Table 1).

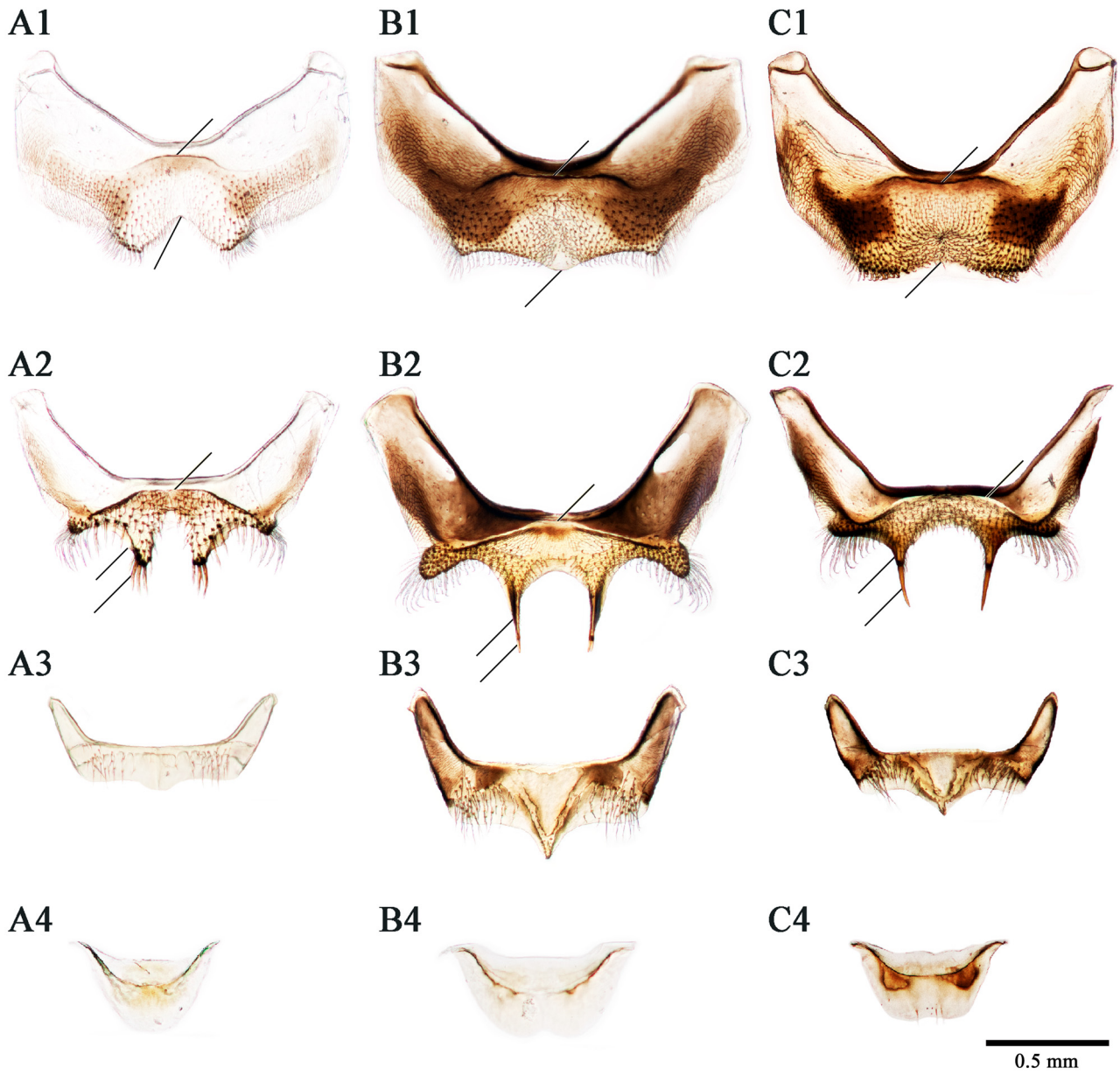

FIGURE 2. Male metasomal sterna, ventral aspect labelled as: (A), (B), and (C) refer to *L. satun* **n. sp.** (Paratype, H.B.-GP3311), *L. flavibasis* (H.B.-GP3322), and *L. doipaensis* (H.B.-GP3183) respectively, with the number following as (1), (2), (3), and (4) refer to S4, S5, S6, and S7 respectively. All subfigures are shown at the same scale and magnification. Diagonal lines indicate the characters treated in the diagnoses.

Description. *Holotype Male*.

Structure: Body length 4.67 mm. Head wider than long; head width 1.77 mm; head length 1.31 mm; eye width (in side view) 0.51 mm; gena width 0.18 mm; interocellar distance 0.31 mm; ocellocular distance 0.17 mm; inner orbits strongly converging below, upper interorbital distance 0.98 mm, lower interorbital distance 0.68 mm; scape length excluding basal bulb 0.48 mm, with basal bulb 0.57 mm; 1st flagellomere length 0.09 mm; 2nd flagellomere length 0.17 mm, width 0.13 mm; 3rd subequal to 2nd; 4th slightly longer than broad; malar space length 0.01 mm; mandible with subapical tooth. Forewing length (measured from humeral angle to apex) 4.03 mm, width 1.52 mm; forewing diagonal 1.1 mm, length of 1st submarginal cell 0.35 mm, 2nd submarginal cell length 0.47 mm, vein Rs

reaching stigma, 1st recurrent vein at approximately mid-length of 2nd submarginal cell. Metatibia length 1.34 mm, width 0.52 mm; metabasitarsus length 0.51 mm, width 0.34 mm.

Metasomal sterna and terminalia are described from paratypes in a separate section below.

Coloration of integument: Head black except as follows: dorsal surface of scape, most of pedicel, proximal half of F1, and small marks towards base and apex of mandible dark brown; supraclypeal area and clypeus brown; labrum, most of mandible, ventral surface of scape, apical mark on pedicel and the rest of F1 yellowish brown. Mesosoma brown except pronotal lobe, mesoscutum, metepisternum and sides of metanotum black and metanotum medially yellowish brown; fore and mid legs pale brown except coxae, trochanters proximally and femora dorsally brown; hind leg brown except tarsus yellowish brown; wings hyaline to pale brown, wing veins and stigma pale brown except veins C, R, M, Rs, and R1 brownish black. Metasomal terga amber brown except T1 with semicircular brown band darker towards sides on disc, basal depression translucent, posterior marginal zone translucent amber, T4–T5 brown; S1 and S2 anteriorly whitish translucent, S3 with lateral brown spot.

Pubescence: Most of face from lower margin of vertex to apex of clypeus with short plumose dense appressed yellowish white hairs; labrum, ventral scape, most portion of genal area, and lower edge of mandible with pale yellowish brown hairs longest at apex of labrum and lower mandible; ventral surface of scape with very short pale brown hairs; vertex with erect long pale yellowish brown hairs, longest hairs of vertex approximately one half as long as scape. Mesoscutum with long and very short pale yellowish brown hairs, the longest hairs approximately one quarter as long as scape; margins of mesoscutum with distinct band of short plumose scale-like yellow hairs interrupted anteromedially and posteriorly; mesoscutellum with pale yellowish brown hairs, progressively longer from anterior to posterior; mesepisternum, metepisternum and metanotum with pale brown hairs, somewhat darker anteroventrally on mesepisternum; posteroventral area of mesepisternum with long white hairs, pronotal lobe and mesepisternum anterodorsally with yellow plumose scale-like hairs; metapostnotum without hairs, lateral surface of propodeum with minute dense white hairs; coxa and trochanter of all legs with long pale brownish white hairs, ventral surface of all femora with pale brown hairs, remaining femora with pale brown hairs intermixed with dark brown hairs, protibia with pale brown hairs intermixed with few short dark brown hairs, the dorsal and anterior mesotibia with dark brown hairs, rest of mesotibia with pale yellowish brown hairs, metatibia dorsally with hairs variable, mostly brown, sometimes dark brown or greyish yellow, or intermixed; protarsus with yellowish brown hairs, meso- and metatarsi with yellowish brown hairs intermixed with few dark brown hairs, posterior surface of metatibia with short yellowish brown keirotrichia. Posterolateral margin of T1 and posterior and lateral parts of T2–T4 with minute sparse pale brownish white hairs; T3–T6 laterally with fine pale brown hairs progressively longer from T3–T6; T7 with pale brown hairs most dense on posterior margin, the longest hairs as long as the longest hairs of T6.

Surface sculpture: Head and most of mesosoma with fine dense punctures; metapostnotum with coarse crowded sharp-edged punctures, diameters 2–2.5 times those of mesoscutum; all legs with fine sparse punctures; metasomal terga shining, T1 with few coarse punctures on posterolateral brown band, T2–T7 with few fine shallow punctures restricted to the posterior margin; metasomal sterna somewhat shining with sparse fine shallow punctures.

Description. ***Paratype Males***, measured as range (Average±SD, n=10). As in the holotype except as follows:

Structure: Body length 4.33–4.85 (4.58±0.15) mm. Head width 1.72–1.77 (1.75±0.02) mm; head length 1.24–1.34 (1.32±0.03) mm; inner orbits converging below, upper interorbital distance 0.94–1.01 (0.97±0.03) mm, lower interorbital distance 0.67–0.73 (0.69±0.02) mm; eye width 0.48–0.54 (0.52±0.02) mm; gena width 0.14–0.18 (0.17±0.02) mm; interocellar distance 0.28–0.31 (0.29±0.01) mm; ocellocular distance 0.18–0.22 (0.2±0.01) mm; scape length excluding basal bulb 0.47–0.52 (0.49±0.01) mm, with basal bulb 0.56–0.59 (0.58±0.01) mm); 1st flagellomere length 0.09–0.11 (0.1±0.01) mm; 2nd flagellomere length 0.15–0.17 (0.16±0.01) mm, width 0.12–0.14 (0.13±0.004); 3rd subequal to 2nd; 4th slightly longer than broad; malar space length 0.01–0.02 (0.01±0.002) mm. Forewing length 3.94–4.09 (4.01±0.05) mm, width 1.47–1.52 (1.49±0.02); forewing diagonal 1.09–1.18 (1.15±0.03) mm, length of 1st submarginal cell 0.3–0.34 (0.32±0.01) mm, 2nd submarginal cell length 0.46–0.52 (0.49±0.01) mm. Metatibia length 1.34–1.43 (1.39±0.03) mm, width 0.47–0.53 (0.5±0.02) mm. Metabasitarsus length 0.47–0.55 (0.5±0.03) mm, width 0.29–0.33 (0.31±0.01) mm.

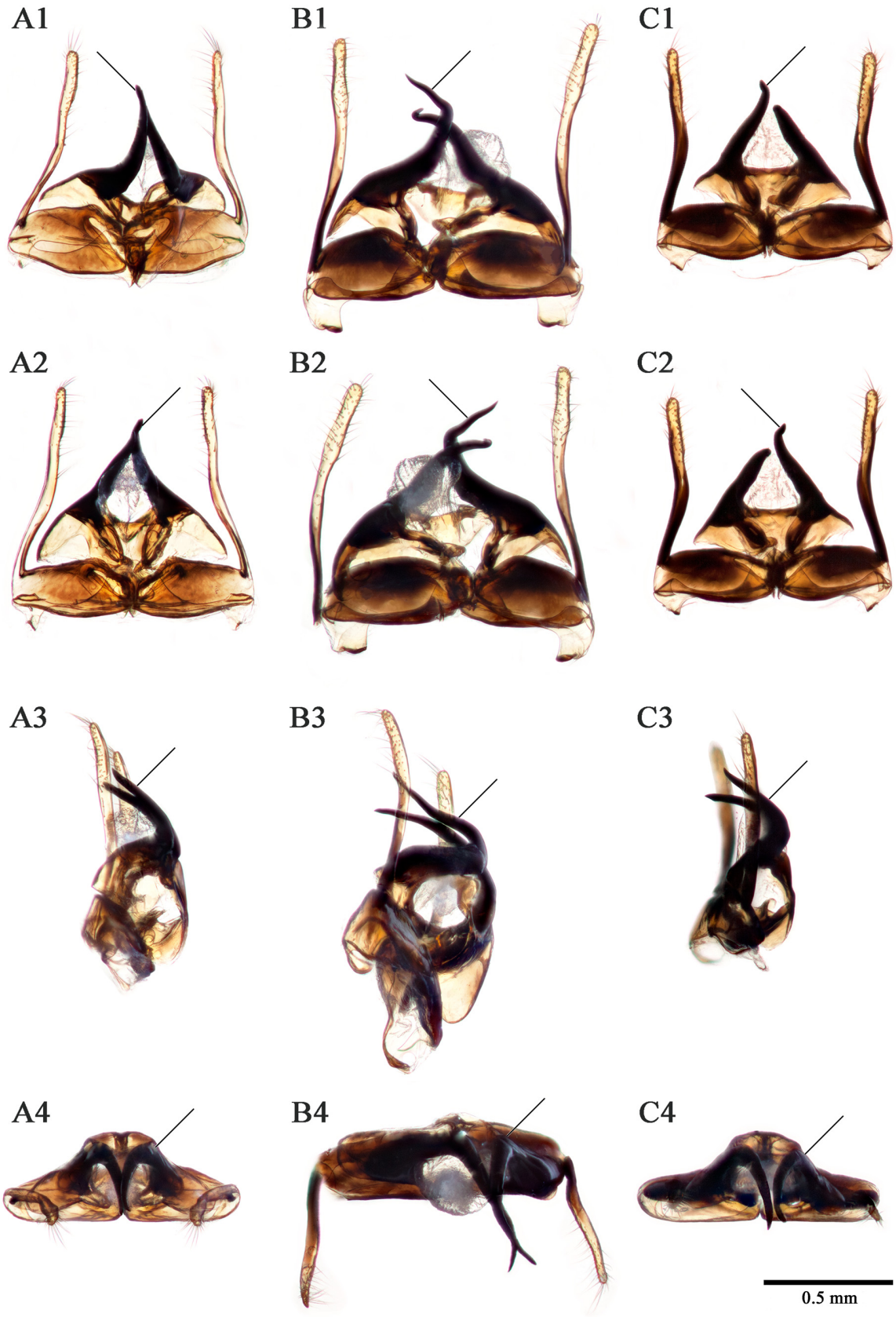

FIGURE 3. Male genital capsules, labelled as: (A), (B), and (C) refer to *L. satun* **n. sp.** (Paratype, H.B.-GP3311), *L. flavibasis* (H.B.-GP3322), and *L. doipaensis* (H.B.-GP3183) respectively, with the number following as (1), (2), (3), and (4) refer to dorsal, ventral, lateral, and caudal aspect respectively. All subfigures are shown at the same scale and magnification. Diagonal lines indicate the right penis valve.

FIGURE 4. *Lepidotrigona satun* **n. sp.**, dorsal habitus. (A) male holotype and (B) worker paratype.

FIGURE 5. *Lepidotrigona satun* **n. sp.**, lateral habitus. (A) male holotype and (B) worker paratype.

Coloration of integument: Ventral scape usually yellowish brown rarely brown on distal half, yellowish brown area on pedicel and 1st flagellomere varies in size, position, and sometimes brown; pale marking on disc of tegula varies in size, seldom absent; mesepisternum sometimes dark brown; propodeum sometimes dark brown or more or less black; all coxae sometimes brown, femora and tibiae vary in darkness of brown; semicircular brown band of T1 varies slightly in width, sometimes darker than other terga; T2–T7 sometimes darker than in the holotype.

Pubescence: Long hairs on vertex, mesoscutum and mesoscutellum sometimes slightly paler and longer than the holotype; yellow plumose scale-like hairs on mesepisternum vary in density; minute hairs on visible portion of metasomal terga vary in length and density.

FIGURE 6. *Lepidotrigona satun* **n. sp.**, head, frontal view. (A) male holotype and (B) worker paratype.

Surface sculpture: Fine shallow punctures on T2–T7 vary in density.

Description. ***Paratype Workers***, measured as range (Average±SD, n=10).

As in the holotype except for usual sexual dimorphism in flagellomeres, metasomal segment number, presence of corbicula, terminalia, and as follows:

Structure: Body length 3.94–4.39 (4.16±0.15) mm. Head wider than long; head width 1.76–1.85 (1.81±0.03) mm; head length 1.38–1.45 (1.41±0.02) mm, inner orbits slightly diverging for upper half, converging below, upper interorbital distance 1.08–1.13 (1.11±0.02) mm, lower interorbital distance 0.97–1.03 (0.99±0.02) mm; eye width 0.41–0.48 (0.45±0.02) mm; gena width 0.2–0.27 (0.25±0.02) mm; interocellar distance 0.27–0.32 (0.29±0.02) mm; ocellocular 0.26–0.3 (0.28±0.01) mm; scape length excluding basal bulb 0.62–0.67 (0.65±0.01) mm, with basal bulb 0.72–0.75 (0.74±0.01) mm; 1st flagellomere length 0.11–0.13 (0.12±0.01) mm; 2nd flagellomere length 0.1–0.13 (0.11±0.01) mm, width 0.11–0.13 (0.13±0.01); 3rd approximate subequal to 2nd; 4th as long as broad; malar space length 0.08–0.11 (0.09±0.01) mm; mandible with two subapical teeth. Forewing length 3.97–4.09 (4.04±0.04) mm, width 1.51–1.54 (1.52±0.01) mm; forewing diagonal 1.15–1.19 (1.17±0.01) mm, length of 1st submarginal cell 0.3–0.34 (0.32±0.01) mm, 2nd submarginal cell length 0.46–0.52 (0.49±0.01) mm, 1st recurrent vein at approximately before middle-length of 2nd submarginal cell. Metatibia length 1.45–1.51(1.49±0.02) mm, width 0.6–0.63 (0.62±0.01) mm; metabasitarsus length 0.57–0.66 (0.61±0.03), width 0.38–0.41 (0.4±0.01). S1 emarginate posteromedially, posterior margin of S2–S5 with shallow broad emargination, S6 entire.

Coloration of integument: Labrum, scape basal bulb, distal and basal marks on scape and 1st flagellomere medially light brown; rest of antenna dark brown (scape and pedicel sometimes black). Mesosoma black except mesoscutellum and tegula dark brown with paler brown disc; all legs black to dark brown, probasitarsus dark to yellowish brown, apex of metatibia and metabasitarsus sometimes brown, tarsi of all legs light brown except slightly darker posteriorly. Semicircular brown band on disc of T1 usually wider laterally than in male; T2–T5 black, sometimes pregradular area of T2 brown; T6 usually black except apex pale, seldom wholly pale brown.

Pubescence: Plumose appressed hairs on face absent from upper frons to vertex, occiput and upper genal area; scape ventrally with few very short pale brown hairs; vertex with erect pale brown hairs shorter and slightly darker than those of male, mesoscutum with sparse short pale brown hairs, medial interruption absent on distinct yellow band; mesoscutellum with long pale yellowish grey hairs variously intermixed with pale to dark brown (but not black) hairs, the thickest hairs about 0.005 mm wide (about 1/10 of the gonostylar width of the male), mesepisternum with fine brown hairs, with long white hairs ventrally, patches of yellow plumose scale-like hairs on mesepisternum anterodorsally and pronotal lobe usually larger than in males; metepisternum and lateral surface of propodeum with fine short pale yellowish white hairs (sometimes yellowish brown); all femora dorsally with dark brown hairs though paler posteriorly, with white (sometimes pale brown) hairs ventrally; pro- and mesotibiae with dark brown hairs intermixed with pale brown hairs posteriorly, metatibia with dark brown hairs dorsally, tips of hairs slightly paler, ventrally with paler hairs intermixed with a few dark hairs, posteriorly with whitish brown keirotrichia; all basitarsi with dark brown intermixed with yellowish brown hairs, remaining tarsomeres with yellowish brown hairs sometimes intermixed with few brown hairs; T1–T4 with minute hairs slightly darker than in male; T3–T6 towards sides with dark brown hairs; S1–S6 with minute pale brown hairs progressively longer from anterior to posterior on each sternum.

Surface sculpture: Punctures on mesoscutellum, metanotum, and metepisternum slightly larger than on rest of mesosoma; all legs mostly with fine punctures intermixed with few coarse punctures, all femora with punctures similar to those of metapostnotum though slightly smaller; anterior surface of metatibia usually shining for ~apical 2/3, shining area varies in size.

Male Metasomal Sterna and Genitalia. In the following, description of genitalic features is based upon dissections of paratype males from all four nests (see material examined). S4–S7 weakly sclerotized except S4 posterolaterally, S5 laterally and posteriorly brown (Fig. 2: A1–4); S4 angularly emarginate apicomedially, depth of emargination ~0.33 times length of sternum, emargination separating two broadly rounded lobes, more strongly sclerotized area of S4 with fine dense hairs, longest and densest lateral to apex of lobe; gradulus of S4 weakly convex close to anterior margin of S4 (Fig. 2: A1); S5 with four apical lobes, long submedian lobes separated by deep U-shaped emargination, depth of emargination ~0.63 times medial length of S5, short lateral lobe separated from medial lobe by shallow concavity, medial lobes bearing ~4–7 thick setae apically, gradulus of S5 transverse medially, near anterior margin (Fig. 2: A2); S6 apical margin weakly produced medially, weakly concave laterally (Fig. 2: A3); S7 1.56 times as wide as long, apical margin convex throughout (Fig. 2: A4). Genital capsule light

brown except black for apical 3/5 of penis valve; penis valve curved ventrally, somewhat hook-like, curvature strongest on basal third to half, then almost straight, the right valve tends to overlap the left one somewhat and its apex is slightly posterior to that of the left valve. Gonostylus not sclerotized, narrow, at least 12 times as long as wide (0.75–0.78 mm long and 0.044–0.058 mm wide), slightly expanded for apical 1/3, medial surface setose on apical half, hairs denser towards apex, lateral surface with few short hairs in apical half (Fig. 3: A1–4).

Etymology. The specific epithet refers to the province in Thailand where the species was collected; it is a noun in apposition.

Material examined. *Holotype*. (Nest TB2, male, to be deposited in QSBG) labelled as follows: "Thaleban Nat. Park/ Satun Prov., 100 m/ 27.iv.2017/ ex nest TB2/ S. THAILAND/ H. Bänziger leg prep det", "HOLOTYPE".

Paratypes. All bearing labels that state "PARATYPE" and the same locality as those of the holotype except dates and nests as follows: Measured paratypes (included in description and Table 1) labelled as follows: 26.iv.2017 (Nest TB1, 1 worker); 27.iv.2017 (Nest TB1, 1 male); 27.iv.2017 (Nest TB2, 3 males, 3 workers); 27.iv.2017 (Nest TB3, 3 males, 3 workers); 27.iv.2017 (Nest TB4, 3 males, 2 workers); 29.iv.2017 (Nest TB1, 1 worker).

Non-measured paratypes: 27.iv.2017 (Nest TB1, 2 males), 26.iv.2017 (Nest TB1, 2 workers), 29.iv.2017 (Nest TB1, 2 workers), 27.iv.2017 (Nest TB2, 17 males, 14 workers; 27.iv.2017 (Nest TB3, 7 males, 2 workers); 27.iv.2017 (Nest TB4, 11 males and 2 workers). Genitalia examined: GP 3304, 3305, 3306, 3308, 3309, 3310, 3311, same nest as holotype; GP 3307, 3312, 3313, 3314, 3315, 3316, 3317, paratypes of nest TB4; GP 3318, 3319, 3320, 3321, 3322, paratypes of nest TB3; GP 3323, paratype of nest TB1.

Male of *L. doipaensis*

***Lepidotrigona doipaensis* (Schwarz, 1939)**, measured as range (Average±SD, n=4).
Figs. 2: C1–4, 3: C1–4 & 7

Diagnosis. Males of *L. doipaensis* can be differentiated from the other two *Lepidotrigona* species of the *L. ventralis* species group known from Thailand as follows (see also diagnosis of *L. satun* above). S4 slightly concave apicomedially (Fig. 2: C1) (strongly concave and convex in *L. satun* and *L. flavibasis* respectively). The apicosubmedial lobes of S5 pointed apically (as in *L. flavibasis*, rounded in *L. satun*), with one very long seta and often a much shorter one (two very short setae in *L. flavibasis*, 4–7 setae of intermediate length in *L. satun*). S4 gradulus touches the antecosta (Fig. 2: C1) (at least slightly separated from the antecosta in the other two species (Fig. 2: A1, B1)). S5 gradulus mostly transverse and touching antecosta medially (Fig. 2: C2) (not touching the gradulus in *L. satun* and doing so only briefly in *L. flavibasis*). Hairs on dorsal surface of metatibia dark brown intermixed with greyish yellow ones (Fig. 7: B) (only greyish yellow hairs in *L. flavibasis*, but variably brown, dark brown or greyish yellow in *L. satun*). The gonostylus and genital capsule are also clearly different in the three species (see descriptions and Fig. 3). The ratio of the forewing diagonal to the length of the 2nd submarginal cell separates all three species (Table 1) and see diagnosis of *L. satun* above.

Description. As for the holotype of *L. satun* **n. sp.** except as follows:

Structure: Body length 4.85–5(4.89±0.07) mm; head width 1.9–1.95 (1.93±0.02) mm; head length 1.42–1.48 (1.45±0.02) mm; eye width 0.55–0.58 (0.57±0.01) mm; gena width 0.18–0.19 (0.19±0.01) mm; interocellar distance 0.39–0.42 (0.4±0.01) mm; ocellocular distance 0.25–0.27 (0.26±0.01) mm; upper interorbital distance 1.08–1.11 (1.09±0.01) mm, lower interorbital distance 0.78–0.8 (0.79±0.005) mm; scape length excluding basal bulb 0.52–0.58 (0.55±0.02) mm, with basal bulb 0.61–0.67 (0.64±0.02) mm; 1st flagellomere length 0.11–0.13 (0.12±0.01) mm; 2nd flagellomere length 0.2–0.22 (0.21±0.01) mm, width 0.13–0.14 (0.14±0.001) mm; 3rd shorter than 2nd; 4th longer than broad; malar space length 0.03–0.04 (0.04±0.001) mm. Forewing length 4.55–4.76 (4.66±0.08) mm, width 1.7–1.76 (1.73±0.02) mm; forewing diagonal 1.28–1.34 (1.3±0.03) mm, length of 1st submarginal cell 0.3–0.32 (0.31±0.01) mm, 2nd submarginal cell length 0.62–0.67 (0.65±0.02) mm. Metatibia length 1.61–1.73 (1.67±0.04) mm, width 0.62–0.66 (0.64±0.01) mm; metabasitarsus length 0.57–0.61 (0.59±0.02) mm, width 0.4–0.41 (0.41±0.005) mm. S4 broadly emarginate apicomedially, depth of emargination 0.15 times length of sternum medially; gradulus of S4 slightly concave medially; S5 apical margin with two long, narrow, acute lobes that delimit an emargination ~0.45 times as deep as length of sternum, emargination approximately as long as wide, submedial lobes each bearing a long, occasionally also a short, thick apical seta, S5

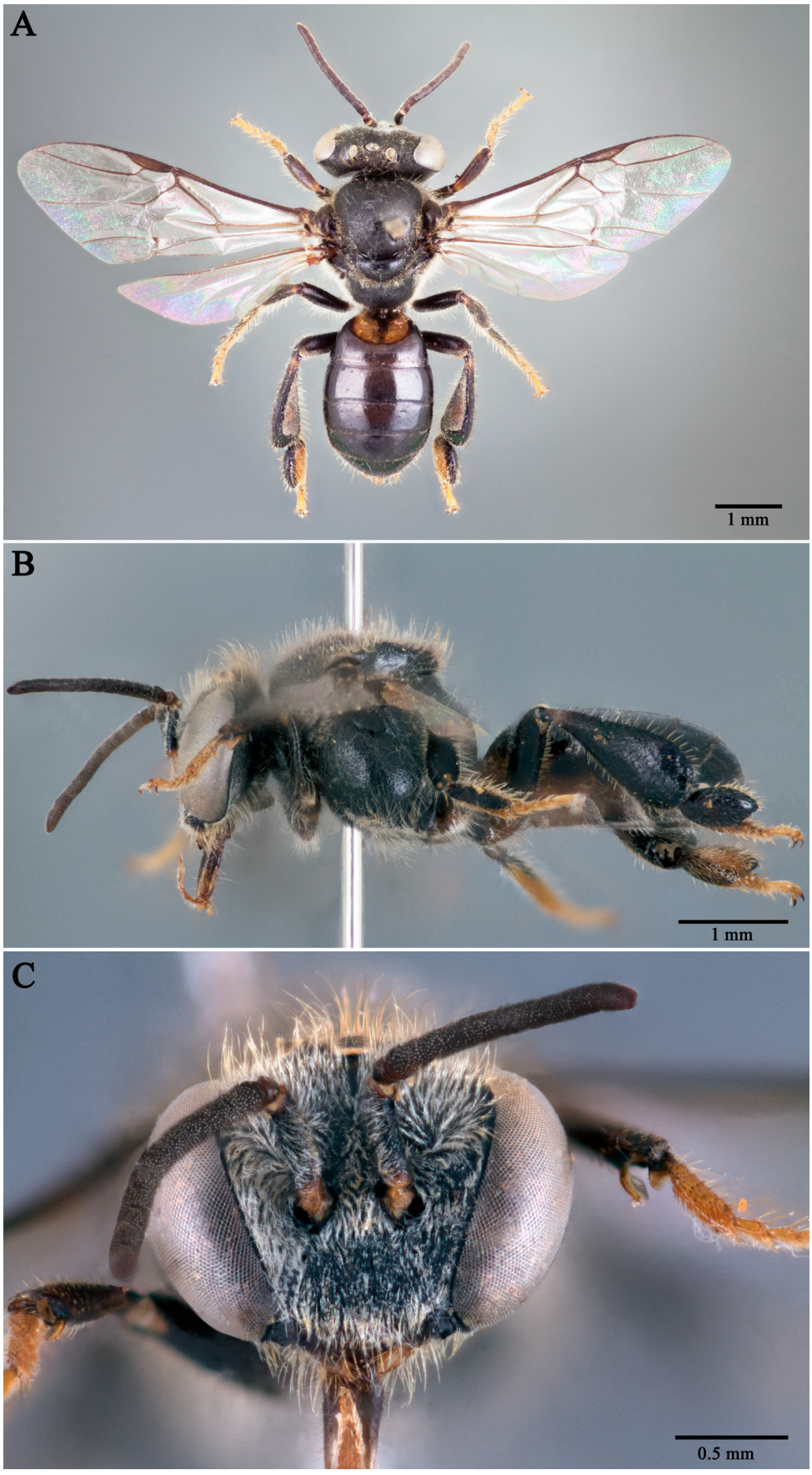

FIGURE 7. Male of *L. doipaensis* from the mountain near the type locality (Doi Suthep, Chang Khian, Chiang Mai, Thailand). (A) dorsal habitus, (B) lateral habitus, and (C) head, frontal view.

gradulus transverse touching antecosta medially; S6 apical margin convex medially with short acute process, S7 ~twice as wide as long, apical margin weakly emarginate, bearing some distinct hairs apicomedially. Genital capsule dark brown to black except base of penis valve, apical half to 2/3 of gonostylus, and gonocoxa anteriorly which are pale brown to brown. Penis valve curved ventrally, curvature strongest on basal third to half, then almost straight, valves normally in contact with each other (exceptionally not so as in Fig. 3: C1–4) and the right valve overarching the left valve. Gonostylus sclerotized basally, medial surface setose on apical ~3/7, approximately 10 times longer than wide (length 0.67–0.71 mm, width 0.062–0.073 mm).

Coloration of integument: Head black except as follows: yellowish brown on basal bulb and extreme apex of scape (sometimes ventral surface of scape entirely yellowish brown); apical 2/3 of mandible; pedicel, and all flagellomeres dark brown. Mesosoma black except tegula; all coxae and femora black; trochanters brown; tibiae brown to black; all tarsi yellowish brown. Metasomal terga dark brown except basal depression and posterior margin of T1 yellowish brown; S1–S3 brown, except S3 laterally dark brown; S4 with large lateral dark brown spot; S5 dark brown apically, paler medially; S6 pale brown except paler on disc; S7 translucent with large lateral mark and gradulus brown.

Pubescence: Face with plumose dense appressed white hairs; frons, vertex, lower genal area, and lower edge of mandible with long pale whitish brown hairs; longest hairs of vertex ~3/4 times as long as scape. Mesoscutum and mesoscutellum with long and very short pale whitish brown hairs, the longest hairs slightly shorter than those of vertex; mesoscutum lacking distinct band of short plumose scale-like yellow hairs; coxa, trochanter, and femora of all legs with pale brownish white hairs; all tibiae with pale brown to greyish yellow hairs, intermixed with short dark brown hairs; metatibia with short dense brownish white keirotrichia.

Surface sculpture: As for male *L. flavibasis*.

Material examined. Type material: *Holotype* (worker, NMNH); Type locality: **THAILAND**; labelled as follows: "Doi Pa/ Mai Deng/ Siam 750m/ 12-29-32", "HughMSmith/ Coll", "TypeNo./ 53563/ U.S.N.M.", "Holotype", "*Trigona ventralis*/ var. *doipaensis*/ H.F. Schwarz", "7080102". [Examined and measured in Table 1]. *Paratypes* (2 workers, AMNH), labelled as follows: "Doi Pa/ Mai Deng/ Siam 750m/ 12-29-32", "HughMSmith/ Coll", "PARATYPE", *Trigona ventralis*/ *doipaensis*/ H.F. Schwarz", "acc 36579". [Examined and measured in Table 1].

Additional material: *Measured male specimens included in description and Table 1 (collected from wild nests):* **THAILAND**, Chiang Mai Prov.: Doi Inthanon, 17.i.2016, K. Attasopa (Nest MYAL5, 2 males); Doi Suthep, Chang Khian stream area, 1020 m, 11.iv.2016, H. Bänziger (Nest CK4, 2 males, caught leaving nest [not swarming]). *Measured worker specimens included in Table 1 (collected from wild nests):* Chiang Mai Prov.: Doi Inthanon, 17.i.2016, K. Attasopa (Nest MKLL1, 1 worker; nest MKLL4, 1 worker; nest MYAL3, 1 worker); Doi Suthep, Chang Khian, 1020 m, 29.ix.2010, H. Bänziger (Nest CK4, 1 worker); Doi Suthep, 26.xii.2015, K. Attasopa (Nest DSTL3, 1 worker). *Non-measured specimens (collected from wild nests):* Chiang Mai Prov.: Chaiprakan, 710 m, 20.ii.2010, H. Bänziger (Nest CP9, 13 workers), 11.iv.2011 (Nest CP26, 4 males, 6 workers, swarming), 16.iv.2016 (Nest CP26, 11 males, 2 workers, caught as leaving nest); Doi Suthep, Chang Khian stream area, 1020 m, 19.iii.2009, H. Bänziger (Nest CK4, 12 workers), 5.viii.2009 (Nest CK4, 4 workers), 19.viii.2009 (Nest CK4, 4 workers), 29.ix.2010 (Nest CK4, 5 workers), 11.iv.2016 (Nest CK4, 10 males, 2 workers, caught as leaving nest); Doi Suthep, Chang Khian stream area, 1040 m, 4.xii.2011, H. Bänziger (Nest CK11, 7 workers), 11.iv.2016 (Nest CK11, 11 males, 3 workers, caught as leaving nest); Doi Inthanon, 17.i.2016, K. Attasopa (Nest MKLL1, 2 workers; nest MKLL4, 2 workers; nest MYAL3, 2 workers); Doi Suthep, 26.xii.2015, K. Attasopa (Nest DSTL3, 2 workers); Doi Suthep, W of temple, 1070 m, 1.iv.2017, H. Bänziger (Nest SHQ1, 8 workers); Doi Suthep northern sector, QSBG area, 25.iii.2010, H. Bänziger (Nest, 13 workers); Hill opposite QSBG, 25.iii.2010, H. Bänziger (Nest in tree trunk, 1 worker); Pa Pä, Ban Huay Phra Chao, 29.vi.2008, H. Bänziger (Nest, 12 workers); North of Chiang Dao Dist., 6.xi.2008, H. Bänziger (Nest TL26, 8 workers), 8.ii.2009, H. Bänziger (Nest TL26, 6 workers).

Genitalia examined: MYAL5-01, MYAL5-02, nest MYAL5, Doi Inthanon, 17.i.2016; GP 3182, 3183, 3191, nest CK4, Chang Khian, Doi Suthep, 11.iv.2016; GP 3179, 3180, 3192, 3258, 3259, 3260, nest CK11, Chang Khian, Doi Suthep, 11.iv.2016.

Comments. Based upon the colour of pubescence, the male of *L. doipaensis* might be misidentified as *L. flavibasis* because it has pale hairs on the vertex and mesoscutellum typical for the worker of the latter species. However, due to the association of the two sexes collected together in the field, the males described above are certainly *L. doipaensis* despite the fact that the hairs are dark in workers of this species.

Male of *L. flavibasis*

***Lepidotrigona flavibasis* (Cockerell, 1929)**, measured as range (Average±SD, n=4).
Figs. 2: B1–4, 3: B1–4 & 8

Diagnosis. *Lepidotrigona flavibasis* differs from the other two species as follows: S4 apicolaterally bisinuate with medial convexity (Fig. 2: B1) (angularly emarginate in *L. satun*, weakly concave in *L. doipaensis* (Fig. 2: A1, C1)); S5 with apicosubmedial lobes pointed apically (as in *L. doipaensis*, rounded in *L. satun*), with one or two very short setae (generally only one very long seta and a much smaller seta in *L. doipaensis* but 4–7 setae of intermediate length in *L. satun*); and S5 gradulus mostly diagonal except short transverse section touching the antecosta medially (Fig. 2: B2) (gradulus parallel to and in touch with most of antecosta medially in *L. doipaensis*, but no contact in *L. satun* (Fig. 2: A2, C2)). *L. flavibasis* also differs in having only greyish yellow hairs on metatibia dorsally (Fig. 8: B) (dark brown intermixed with greyish yellow hairs in *L. doipaensis*, but variably brown, dark brown or greyish yellow hairs in *L. satun*). The ratio of the forewing diagonal to the length of the 2nd submarginal cell separates *L. flavibasis* from *L. satun* (see diagnosis of *L. satun* above and Table 1). The gonostyli and penis valves are also clearly different in the three species (see descriptions and Fig. 3).

Description. As for the holotype of *L. satun* **n. sp.** except as follows:

Structure: Body length 4.8–4.94 (4.91±0.07) mm. Head width 1.76–1.78 (1.78±0.01) mm; head length 1.34–1.37 (1.35±0.01) mm; eye width 0.56–0.57 (0.56±0.005) mm; gena width 0.18–0.2 (0.19±0.01) mm; interocellar distance 0.34–0.35 (0.35±0.01) mm; ocellocular distance 0.2–0.22 (0.21±0.01) mm; upper interorbital distance 1.1–1.11 (1.1±0.01) mm, lower interorbital distance 0.75–0.78 (0.77±0.01) mm; scape length excluding basal bulb 0.51–0.52 (0.51±0.005) mm, with basal bulb 0.57–0.59 (0.58±0.01) mm; 1st flagellomere length 0.08–0.13 (0.11±0.02) mm; 2nd flagellomere length 0.17–0.18 (0.18±0.005) mm, width 0.14–0.15 (0.14±0.004) mm; 3rd slightly shorter than 2nd; 4th longer than broad; malar space length 0.03–0.04 (0.03±0.005) mm. Forewing length 4.39–4.48 (4.42±0.04) mm, width 1.6–1.61 (1.6±0.01) mm; forewing diagonal 1.23–1.29 (1.26±0.03) mm, length of 1st submarginal cell 0.3–0.33 (0.31±0.01) mm, 2nd submarginal cell length 0.58–0.61 (0.6±0.01) mm. Metatibia length 1.4–1.42 (1.41±0.01) mm, width 0.54–0.56 (0.55±0.01) mm; metabasitarsus length 0.58–0.59 (0.59±0.01) mm, width 0.37–0.39 (0.38±0.01) mm. S4 convex apicomedially, gradulus of S4 weakly concave medially, with small apicolateral angulation; S5 apical margin with two long, narrow processes bearing one or two very short thick setae, processes delimit an emargination ~0.54 times as deep as length of sternum and as long as wide, apicolateral lobe well developed, bearing long curved setae, gradulus touching antecosta medially; S6 with acute triangular apicomedial process; S7 approximate twice as wide as long, apical margin weakly emarginate. Genital capsule dark brown to black except base of penis valve, apical half to 2/3 of gonostylus and gonocoxa anteriorly pale brown to brown; the right penis valve overarches the left one and has two right angles directed to the right, so that the tip of the valve ends to the right of the midline of the bee, and generally posterior and often dorsal to the tip of the left penis valve. In the left penis valve the first angle is less acute and the second angle is missing but replaced by a curvature directed to the right, hence also bringing the tip of the left valve to the right of the midline, the tip is anterior and often ventral to the tip of the right penis valve. In addition, the final fourth or fifth of the valves is sinuous, the tips diverging from each other. Gonostylus sclerotized basally, approximately 12 times longer than wide (length 0.91–0.96 mm, width 0.073–0.080 mm) hairs equally dense throughout the apically expanded portion.

Coloration of integument: Head black except as follows: yellowish brown on basal bulb and extreme apex of scape, labrum, and apical half of mandible; F2–F11 dark brown. Mesosoma black except pronotal lobe and tegula dark brown; fore and mid legs dark brown except medio- and distitarsi yellowish brown; hind leg black except tarsus yellowish brown (sometimes metabasitarsus dark brown). Metasomal terga black except basal depression of T1 transparent brown and apex of T6 and T7 brown. S1–S3 dark brown except posterior half of S1, posterior margin of S2, and apex of S3 whitish translucent; S4 brown except apical margin and most of disc medially translucent; S5 with apical and apicolateral lobes brown; S6 with anterolateral brown spot; S7 translucent except gradulus narrowly brown.

Pubescence: Face with short plumose dense appressed white hairs; vertex with erect long pale whitish brown hairs. Mesoscutum with long and very short pale whitish brown hairs; mesoscutum, pronotal lobe and mesepisternum lacking distinct band of short plumose scale-like yellow hairs on margins; mesoscutellum with erect long pale whitish brown hairs longest on posterior margin; mesepisternum, metepisternum and metanotum with brownish white hairs; coxa and trochanter of all legs and ventral surface of all femora with long pale brownish

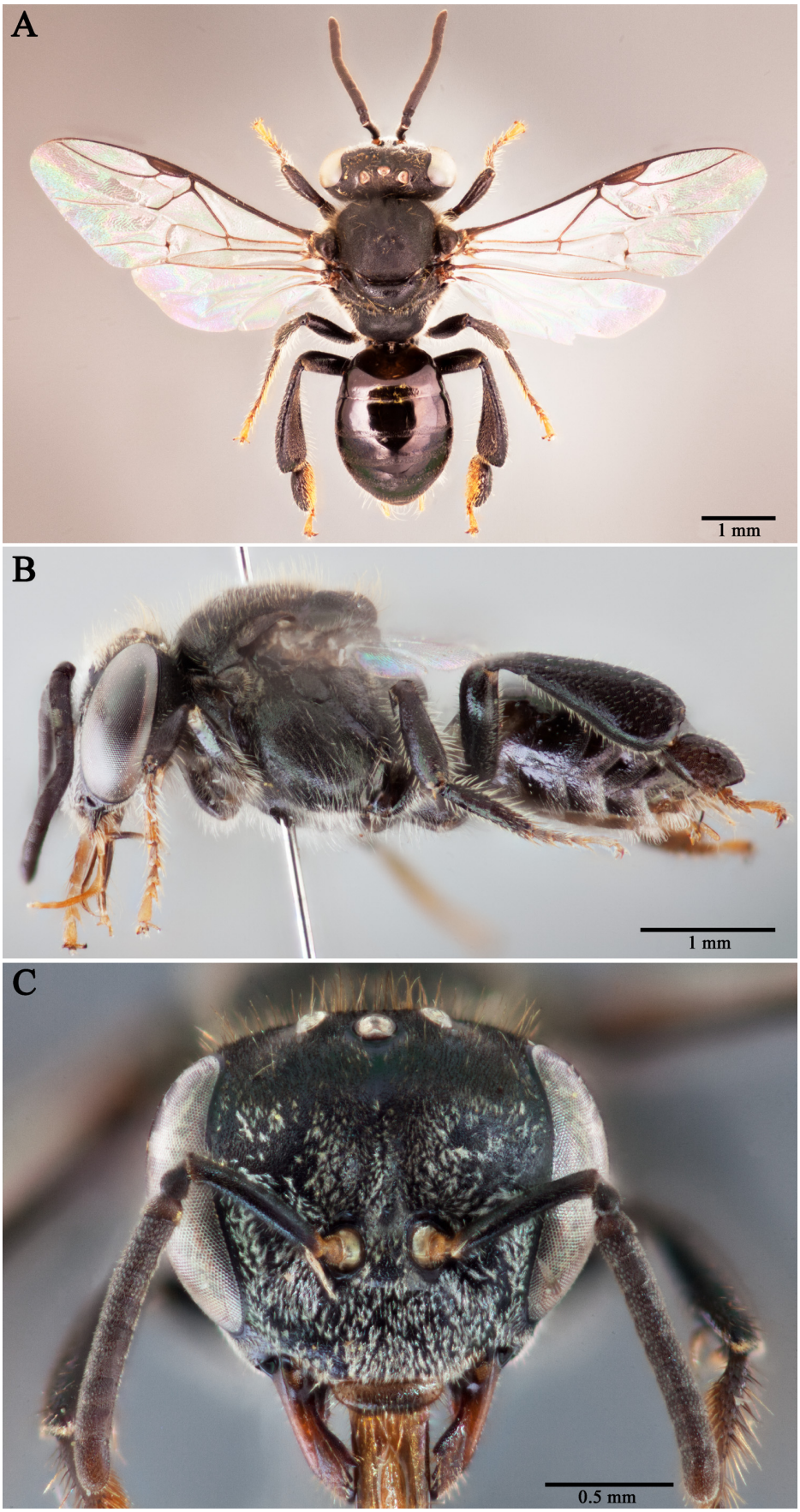

FIGURE 8. Male of *L. flavibasis* from the type locality (Doi Suthep, Chang Khian, Chiang Mai, Thailand). (A) dorsal habitus, (B) lateral habitus, and (C) head, frontal view.

white hairs, rest of femora with brownish white hairs intermixed with pale brown hairs; pro- and mesotibiae with dark brown hairs intermixed with brownish white hairs; metatibia with short greyish yellow hairs, coloration and density approximately the same on dorsal and ventral margins; all tarsi with whitish brown hairs intermixed with yellowish brown hairs, metatibia with short sparse brown keirotrichia. Posterolateral margin of T3–T7 with fine brownish white hairs progressively longer from T3–T7.

Surface sculpture: All legs with fine dense punctures. T1 with sparse fine shallow punctures except impunctate on basal depression; metasomal sterna with coarse shallow crowded punctures intermixed with sparse coarse punctures.

Material examined. Type material: *Holotype* (worker, AMNH); Type locality: **THAILAND**; labelled as follows: "Doi Sutep./Siam/ Feb. 9/ Alice Mackie", "*Trigona/ flavibasis*/ TYPE. CKll", "acc 35740". [Images examined (provided by AMNH, 2017)].

Additional material: *Measured male specimens included in description and Table 1 (collected from wild nests):* **THAILAND**, Chiang Mai Prov., Doi Suthep: 6.iv.2017, H. Bänziger (Nest SHQ2, 4 males, caught leaving nest [not swarming]). *Measured worker specimens included in Table 1 (collected from wild nests):* Chiang Mai Prov.: Doi Suthep, 26.xii.2015, K. Attasopa (Nest PHPL1, 2 workers); Doi Suthep-Pui, 1080 m, 6.iv.2017, H. Bänziger (Nest SHQ2, 2 workers). *Non-measured specimens (collected from wild nests):* Chiang Mai Prov.: Doi Inthanon, 17.i.2016, K. Attasopa (Nest MYAL1, 3 workers; MKLL3, 3 workers); Doi Suthep, 26.xii.2015, K. Attasopa (Nest DSTL1, 2 workers; nest PHPL1, 3 workers); Doi Suthep-Pui, 1080 m, 1.iv.2017, H. Bänziger (Nest SHQ2, 6 workers), 6.iv.2017, H. Bänziger (Nest SHQ2, 16 males, 9 workers, caught leaving nest [not swarming]). *Non-measured specimens (collected by H.B. while they sucked his sweat):* Chiang Mai Prov., Doi Inthanon, above Mae Ya Noi, 1700 m, 22.ii.1993 (4 workers).

Genitalia examined: GP 3296, 3297, 3298, 3299, 3300, 3301, 3302, nest SHQ2 of type locality, Doi Suthep, 6.iv.2017.

TABLE 1. Measurement of malar space length (MSL), F1 length (F1L), metatibia width (MTW), forewing diagonal (FWD), and 2nd submarginal cell (SM2L) ratios that separate *L. satun* **n. sp.**, *L. flavibasis*, and *L. doipaensis*, expressed as range (Average±SD). Holotype ratios in bold.

	L. satun **n. sp.**	*L. flavibasis*	*L. doipaensis*
Male characters	n = 10 paratypes from 4 nests	n = 4, 1 nest from type locality	n = 4, 2 nests near type locality
MSL to F1L	**0.13**/0.1–0.16 (0.13±0.02)	0.3–0.34 (0.31±0.02)	0.27–0.33 (0.29±0.02)
MSL to MTW	**0.02**/0.02–0.03 (0.03±0.004)	0.05–0.07 (0.06±0.01)	0.05–0.06 (0.06±0.002)
FWD to SM2L	**2.32**/2.3–2.53 (2.41±0.07)	2.05–2.11 (2.09±0.02)	1.94–2.05 (2±0.05)
Worker characters	n = 10 paratypes from 4 nests	n = 8, 5 nests from type locality	n = 8, holotype and 2 paratypes and the rest from 5 nests, near type locality
MSL to MTW	0.13–0.17 (0.15±0.02)	0.23–0.25 (0.23±0.01)	0.18–0.19 (0.18±0.01)
FWD to SM2L	2.29–2.51 (2.37±0.06)	2–2.14 (2.07±0.05)	1.98–2.19 (2.09±0.06)
MTW to SM2L	1.21–1.33 (1.25±0.04)	0.88–0.98 (0.92±0.04)	1.05–1.09 (1.08±0.02)

Additional material of other species of *Lepidotrigona* (all studied by us unless stated otherwise)

L. ventralis:

Type material: *Holotype* (worker, BMNH); Type locality: **MALAYSIA**: "Borneo (Sarawak)". [Not examined].

Additional material: **MALAYSIA**, Borneo, Sarawak, Gunung Buda, 20–28.xi.1996, A. D. Mudge (2 workers, PCYU); **INDONESIA**, W. Kalimantan, Gunung Palung Nat. Pk. 17–29.vi.1991, C. Darling, U. Rosichon, H. Sutrisno (3 workers, PCYU); W. Kalimantan, Gunung Palung Nat. Pk. 15.vi–15.vii.1991, C. Darling, U. Rosichon, H. Sutrisno (9 workers, ROM).

L. hoosana:

Type material: *Holotype* (worker, AMNH); Type locality: **TAIWAN**; labelled as follows: "Formosa/ Taihorin. III.10/ H.Sauter S.G.", "*T. ventralis hoosana*/ 1925 Friese det.", "AMNH_IZC 00324480", "acc 35178", "Holotype", "*Trigona/ ventralis*/ var. *hoosana*/ H.F. Schwarz". [Examined].

L. arcifera:
Type material: *Holotype* (worker, BMNH); Type locality: **INDIA**; labeled as follows: "Type", "B.M. TYPE/ HYM./ 17B.1081", "*Trigona*/ *arcifera* Ckll/ TYPE", "*Trigona*/ *ventralis Sm*/ *(worker) from Sladen*.", "Teesta/ Bridge/ Himalayas/ India/ 10.1.97", "T.D.A. Cockerell./ B.M.1936-415.". [Images examined (Fig. 2 and Table 1 of Rasmussen, 2013)].

Discussion

Notes on the type localities of *L. flavibasis* and *L. doipaensis.* The type locality of *L. flavibasis* is unambiguous, it is "Doi Suthep" and we have both workers and associated males from this site. The morphological differences between our males and those described by Sakagami (1975) from Vietnam suggested to belong to *L. flavibasis* (as *Trigona* (*Lepidotrigona*) *ventralis flavibasis*) are sufficient for us to believe that the males he described represent an undescribed species (see below). The situation is more complex for *L. doipaensis*. We have been unable to find its exact toponym 'Doi Pa, Mai Deng, Siam, 750 m' where Hugh M. Smith collected the holotype on 29.xii.1932. However, 'Doi' is unmistakably a northern Thai word meaning 'hill' or 'mountain'. In maps it is exclusively used in upper North Thailand: the provinces of Mae Hongson, Chiang Mai, Chiang Rai, Phayao, Nan, Lamphoon, Lampang, Phrae, Uttaradit, and the northern half of Tak. These encompass a trapezoidal area of about 300 by 350 km. We believe that the type locality of *L. doipaensis* must be within this area within which the Chiang Mai valley and surrounding mountains occupy an approximately central location. Further, we assume that in the lack of a name for this 'Doi', Hugh Smith decided to denote it with the name of a near-by village, viz. 'Pa Mai Deng'. There is a 'Ban Pa Mai Daeng' ('Ban', term used for 'village', 'Daeng' is the modern spelling for 'Deng' with the same pronunciation, meaning 'red', 'Pa Mai' meaning 'forest') 17 km NE of Chiang Mai. Significantly, some 9 km SE of this village is an unnamed hill 751 m in altitude. We propose this to be the most probable type locality of the species. We collected workers and males from several nests in the hills surrounding Chiang Mai, and the type locality is well within this area. It is also worth noting that workers and males from Ban Pa Mai Daeng and surroundings do not differ morphologically, and only minimally genetically (Attasopa, Bänziger, Disayathanoowat & Packer, unpublished data), from conspecifics from Doi Suthep, the precise type locality of *L. flavibasis* and where the two species are sympatric.

Sakagami's *L. flavibasis* as an undescribed species. Males ascribed to *L. flavibasis* [as *Trigona* (*Lepidotrigona*) *ventralis flavibasis*] from Vietnam by Sakagami (1975) are the only previously known males of the *L. ventralis* species group. Our reasons for deciding that the Vietnamese specimens are not true *L. flavibasis* are as follows. First, Sakagami (1975) states male "posterior fringe of metatibia dark brown" in contrast to the greyish yellow hairs in *L. flavibasis* (from all localities where males are known, including the type locality – see Material Studied for this species above). Second, the apicomedial concavity of S5 is clearly deeper than the sublateral concavity and almost twice as deep as its own apical width in Sakagami's specimens (his Fig. 13) whereas in our material the apicomedial concavity is shallower than the sublateral ones with its depth and width subequal (Fig. 2: B2). Third, the apicomedial lobe of S6 of Sakagami's male is clearly obtuse and the longest hairs arise at the extreme apicolateral margin (his Fig. 13). In contrast, males of what we consider to be true *L. flavibasis* have this lobe acute and with the longest hairs removed from the apicolateral extremity (Fig. 2: B3). Fourth, although he only drew one half of the genital capsule, the penis valve in Sakagami's Fig. 14 is evenly curved whereas it is strongly sinuous in *L. flavibasis*. Additional study of this material would be important.

Male genitalic asymmetry. We note the asymmetry in the genitalia of the three species described above. Asymmetry in genitalia is unusual among bees, best known in the genus *Tarsalia* where S7, S8 and aspects of the genital capsule are asymmetrical (see figures in Baker 1998, Figs. 31–36; Engel *et al.* 2017a, Fig. 5). Thus, according to Michener (2007) who states that such asymmetry is unique to *Tarsalia*, we document here the second independent origin of male genitalic asymmetry among the bees.

The degree of asymmetry among our three species differs considerably. It is most strongly developed in *L. flavibasis* in which both penis valves are strongly curved to the right (in dorsal aspect) for their apical ~1/3 (Fig. 3: B1–4). In *L. doipaensis* and *L. satun* **n. sp.** the penis valves are shorter and the curvatures less pronounced. The asymmetry is weakest in *L. satun* **n. sp.**

It is also worth noting that without exception, all the many genitalia of *L. flavibasis* studied herein were

asymmetric in the same way and were even positioned asymmetrically when still inside the metasoma. Thus, the penis valves were always in the position as shown in Fig. 3: B1–2, even when at rest, still naturally inside the metasoma. The tip of the right valve (as seen in Fig. 3: B1) is posterior to the left one. The position shown is not an artifact resulting from dissecting or mounting.

While we cannot be certain of the function of genitalic asymmetry, as is generally the case with animal genitalia (Eberhard 1985), sexual selection would likely be the cause.

Final Comments on the *Lepidotrigona ventralis* species group. Our data clearly demonstrate that what has been considered by some to be a single (Ascher & Pickering 2017), albeit perhaps variable (Sakagami 1975), species termed *L. ventralis*, is a complex of species (as recognized by Rasmussen 2008) whose members are readily differentiable using pubescence coloration characteristics, morphological measurements and, where males are available, details of male metasomal sterna and genitalia. The male external metasomal sterna and the genital capsules of *L. satun* **n. sp.** provide excellent characters for species delimitation, and also permit the differentiation of other species in the *L. ventralis* group: *L. flavibasis* and *L. doipaensis* and the undescribed species thought to belong to the former by Sakagami (1975). We encourage others to make the, often considerable, effort required to find males of Meliponini from nests, as our data suggest they may often have more diagnostic species level characters than do the workers, as has been noted by others (Schwarz 1939; Sakagami 1975, 1978; Sakagami & Inoue 1978; Camargo & Moure 1994; Camargo *et al*. 2000; Gonzalez & Griswold 2011, 2012; Dollin *et al*. 2015; Halcroft *et al*. 2016; Engel *et al*. 2017b). However, we would argue against nest destruction in order to find them: all the males we describe here were collected as they left the nest entrance associated with conspecific nestmate workers. *Lepidotrigona ventralis* differs from the new species not only by morphology of the holotype as indicated in the original description by Smith (1857), Schwarz's (1939) identification key (as *L. ventralis* s.s.), and the holotype examined by Rasmussen (2016, pers. comm. with H.B.), but also our examined museum specimens from the type locality and nearby areas, in which all the hairs on the dorsal surface of the metatibia are white.

There are biogeographic differences between the new species and the others in the *L. ventralis* species group in Thailand. The new species' nests were discovered from a low altitude area, 100 m a.s.l. in Satun province, which is around 480 km away from the Isthmus of Kra to the South. Kra is a biogeographically important region; it is an ecotone between the evergreen forests south of it and the forests with a marked dry season north of it (van Steenis 1950; Woodruff 2003). In contrast, *L. doipaensis* and *L. flavibasis*, for which type material and our own specimens agree, come from higher altitudes, of at least 500–1100 and 925–1700 m a.s.l. respectively in northern Thailand, some 1,300 km north of Satun. Moreover, *L. ventralis* itself is known only from the island of Borneo which is at least 1,200 km across the South China Sea from the type locality of the new species. Although *L. ventralis* s.s. has been recorded from several other countries, including Thailand (as listed in Rasmussen 2008), Schwarz (1939) never verified this species from anywhere except the type locality. All supposed *L. ventralis* s.s. H.B. has seen from Thailand were misidentified.

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